

Symposium

Selection for Resistance in Invasive Plants¹

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Abstract: Although evolution has been neglected in invasive species work, evolutionary theory can be used to guide invasive species management, and research on exotic species can be used to test evolutionary theory. One substantial challenge in invasive plant management is the evolution of resistance to herbicides, biological control, and other treatments. We show how the tools of quantitative genetics and selection analysis can be used to investigate the potential for evolution of resistance, which can aid in the management of invasive plant populations. We also illustrate how invasive species research can be used to test theory, such as the evolution of increased competitive ability hypothesis. We outline the methods to investigate this theory and recommend including evolutionary considerations in invasive species management.

Additional index words: Biological control, genetics, herbivory, natural enemies, *Melaleuca quinquenervia* MLAQ.

Abbreviation: EICA, evolution of increased competitive ability.

EVOLUTION IN INVASIVE PLANTS

Invasions by exotic plants pose one of the greatest threats to natural systems (Mooney and Hobbs 2000; Pimentel 2002). They also offer a unique opportunity to study ecological and evolutionary processes (Allendorf and Lundquist 2003). Although the ecology of exotic plant invasions has received much attention, their evolutionary implications have been considered less frequently (Allendorf and Lundquist 2003; Hanfling and Kollmann 2002; Stockwell et al. 2003). In this article, we explain why invasive species management should consider evolution, highlight evolutionary questions that can be addressed using invasive systems, and use our research on biological control and herbivore resistance in the invasive plant melaleuca [*Melaleuca quinquenervia* (Cav.) S.T. Blake] to illustrate some of the methods that can be used to explore evolution in invasive species.

Management treatments such as herbicides or biological control can impose strong selection for resistant genotypes, causing them to spread through the population and potentially reduce the efficacy of management techniques. The evolution of resistant genotypes could be

one of the most substantial and important threats to the long-term, sustainable management of invasive and other problematic species (Allendorf and Lundquist 2003; Holt and Hochberg 1997); yet, evolution is rarely considered in management planning, research, and decision making (Parker et al. 2003). Evolutionary theory, specifically the analytical methods of quantitative genetics and selection analysis, offers a powerful set of tools for predicting how traits such as herbicide resistance are expected to change with time. We briefly illustrate these techniques and outline how they can be used to investigate the evolution of resistance in invasive plants.

The focus of evolutionary analysis is the traits or set of traits of individuals. Many important traits vary continuously, and these are called quantitative traits. Quantitative genetics deals with the inheritance patterns of quantitative traits. Examples of quantitative traits include the density of hairs (trichomes) on leaf surfaces or the tissue concentration of a defensive chemical. For simplicity, we will initially focus on a single trait, leaf trichome density. The hair density measured on the leaves of a single plant is that individual's trait value for trichome density. In the simplest case, the potential for trichome density to evolve in response to selection is determined by three factors: (1) the variability in trichome density among individuals in the population (variation), (2) the extent to which individual variation is genetically controlled (heritability), and (3) the degree to which an individual's trichome density influences its rel-

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ative contribution of progeny to future generations (differential fitness).

Evolutionary response can be expressed by the breeder's equation

$$R = h^2S \quad [1]$$

in which the response to selection, R , is the change in average trait value between the offspring and parental generations. The selection differential, S , is the difference in the average trait value before and after selection (Falconer and Mackay 1996). Heritability, h^2 , is a measure of the degree to which offspring trait values resemble those of their parents because of inherited genes.

To estimate the heritability of a trait, various methods can be used that incorporate information about the degree of relatedness among individuals to partition trait variance in the sample population into causal components. These methods include sib analysis and parent-offspring regression and are detailed in quantitative genetics texts such as Falconer and Mackay (1996) and Lynch and Walsh (1998). The variance among individuals in any quantitative trait can be partitioned according to the following equation:

$$V_P = V_E + V_G \quad [2]$$

where V_P is total phenotypic variance, V_E is variation due to environmental factors, and V_G is variation due to genetic factors (Falconer and Mackay 1996). V_G can further be partitioned into components due to additive genetic factors and to nonadditive factors including dominance, epistasis, and cytoplasmic effects. Only the additive genetic variance, V_A , of a trait contributes to its narrow-sense heritability (h^2):

$$h^2 = V_A/V_P \quad [3]$$

To examine the potential for resistance traits in an exotic species to evolve in response to management treatments, such as herbicides or biological control agents, it is necessary to ascertain the genetic variance and covariances among the traits and the intensity of selection on the traits (Simms and Rausher 1992), which can be done with split-brood experiments (e.g., Rausher and Simms 1989). For such experiments, it is first necessary to obtain a population of known or estimated relatedness, through experimental crosses, or a collection of seeds of known maternity (Falconer and Mackay 1996), or by using molecular markers (Ritland 2000). Sample size must be adequate to estimate the quantitative genetic parameters. Ideally, field-collected seeds should be raised in a common environment for at least one generation to

reduce maternal environmental effects. Next, using an appropriate experimental design, apply the management treatment to one half of each genetically related group (e.g., maternal family), leaving the other half untreated. Record data on initial plant conditions, effectiveness of the management treatments, and any traits of interest. Traits might be complex, such as resistance (ability to minimize damage) and tolerance (ability to maintain performance despite damage), as well as specific characters such as leaf toughness, trichome density, or concentrations of potentially defensive compounds. Also record an estimate of fitness, such as total biomass or flower or seed number. Calculate genetic variances and covariances from the degrees of observed resemblance between individuals of differing known degrees of relatedness (Falconer and Mackay 1996). Genetic correlations among traits may also be estimated from correlations among breeding values (Falconer and Mackay 1996). Estimate the pattern and strength of selection by regressing breeding values on fitness estimates (Falconer and Mackay 1996; Lande and Arnold 1983; Rausher 1992). If resistance is heritable and positively correlated with fitness under management treatment conditions, then the evolution of resistance in wild populations subjected to this treatment may be expected, and managers may plan control strategies accordingly.

In addition to predicting the evolution of resistance, appropriately designed experiments can test theory in invasive plant ecology and evolution. For example, the evolution of increased competitive ability (EICA) hypothesis proposes that exotic plant species may become invasive in part by escaping their natural enemies and that these conditions relax selection for herbivore defenses, resulting in an overall increase in competitive ability in the new range (Blossey and Nötzold 1995). In the following section, we develop the motivation for this hypothesis, outline how it can be tested, and illustrate such an investigation with our research on the effects of biological control insect herbivory on the invasive plant *melaleuca*.

SELECTION, RESISTANCE, AND NATURAL ENEMY ESCAPE

Release from herbivory has been invoked as a major reason for the success of some invasive plants (Keane and Crowley 2002). Relaxation of herbivore pressure may also result in changes in the patterns of selection on plant defense and competitive ability traits, as posited by the EICA hypothesis (Blossey and Nötzold 1995; Cox 1999; Maron and Vilá 2001). The EICA hypothesis pro-

poses that in their native range, plant population density is regulated in part by herbivores or other natural enemies such as pathogens. Native plant populations are also well defended because of selection imposed by herbivores. In the introduced range, specialist herbivores are absent, allowing populations of the exotic plant to escape regulation and increase to high densities. The absence of herbivory also relaxes selection for resistance. Moreover, if, as proposed by plant-herbivore theory, resistance involves a fitness cost, then plants lacking defenses may be more fit in the absence of herbivores. Thus, if they are heritable, defensive traits would be expected to decline in the new range. Some predictions of the EICA hypothesis are as follows: (1) insects should prefer and cause greater damage to plants from the new range, (2) plants from the home range should be more resistant, (3) resistance traits should be heritable, and (4) resistance traits should correlate positively with fitness in the presence of herbivores and negatively in the absence of herbivores. Recent research both supports (Daehler and Strong 1997; Siemann and Rogers 2003; Wolfe 2002) and refutes (Agrawal and Kotanen 2003; Vilá et al. 2003; Willis et al. 1999) various predictions of the EICA hypothesis, with more work in this area clearly needed.

To illustrate how studies can be conducted to determine whether an invasive plant may evolve resistance to management treatments and to test evolutionary theory, we outline the methods we are using in our research on melaleuca. Melaleuca is one of the most invasive weeds in the Florida Everglades (Turner et al. 1998), possibly in part because of the fact that the hundreds of insect species that feed on the plant in its native range of eastern Australia and New Caledonia are absent in Florida (Balciunas and Burrows 1993; Burrows and Balciunas 1999). Two insects have been released in Florida as melaleuca biological control agents: *Oxyops vitiosa* (Coleoptera: Curculionidae) Pascoe, a leaf-chewing weevil, and *Boreioglycaspis melaleucae* (Hemiptera: Psyllidae) Moore, a sap-feeding psyllid (Pratt et al. 2002).

We are conducting a split-brood experiment to determine the effects of the biological control insects on melaleuca plants from Australian and Floridian source populations. Seed capsules were collected from trees in Australia (native habitat) and in Florida (introduced habitat). We started seedlings from these maternal families in flats and transplanted established seedlings to a common garden. Representatives from each maternal family were split between two treatment groups: a control, exposed to natural infestation by locally occurring populations of the biological control agents, and an insecticide treat-

ment. We measure plant performance (height, leaf number, and survival), herbivore impact (presence or absence of each insect species, proportion of total leaf area damaged), and leaf traits potentially related to defense (leaf toughness, pubescence, and terpenoid and nitrogen contents). Levels of herbivore impact and defensive traits on genotypes from Florida and Australia are being compared to test EICA predictions that plants from the introduced range should be preferred, suffer greater insect damage, and show decreased levels of defense compared with plants from the home range. Quantitative genetic and selection analyses are being used to measure heritabilities, genetic correlations, and selection on traits to predict whether resistance is likely to evolve in response to herbivory by the biological control agents.

The procedures outlined here can be used for invasive weeds and other species of concern to help managers determine whether the plants are likely to develop resistance to biological control herbivory or other treatments. These studies can also be used to test ecological and evolutionary theories such as the EICA hypothesis. With studies of additional species, it will be possible to develop a better understanding of evolution in plants in general and invasive weeds in particular and to draw broader conclusions regarding the conditions under which the evolution of resistance is likely to occur.

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